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PREDATORY BEHAVIOR OF *TETRAGNATHA PRAEDONIA* (ARANEAE: TETRAGNATHIDAE)

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Synopsis

Yoshida, M. (Department of Biology and Geology, Faculty of Science and Engineering, Ritsumeikan University, Kyoto 603, Japan) : Predatory behavior of *Tetragnatha praedonia* (Araneae: Tetragnathidae). *Acta arachnol.*, **35**: 57-75 (1987).

The predatory behavior of *Tetragnatha praedonia* was studied. The prey consisted of mainly Diptera, especially midge flies, smaller than 3 mm in body length. When capturing small prey, this species applied mainly "Seize-Pull out" strategy to them; that is, it plucked the web to locate the prey, ran and seized it in the jaws, pulled it out of the web, then carried to the hub and fed there. When given large prey more than 5 mm, this species captured them by various strategies. It captured Lepidoptera mainly by "Bite-Wrap" strategy; that is, the prey was immobilized by bite, then was wrapped with silk. On the other hand, craneflies and damselflies were captured by three strategies, that is, "Seize-Pull out", "Bite-Wrap" and "Wrap-Bite". In "Wrap-Bite" strategy, the prey were attacked by wrapping, then bitten by the spider. But, the wrapping seemed to be of little use to immobilize the prey, because this species used the silk with less adhesiveness and did not used the swathes of silk.

It was verified that this species can use all the strategies which are used by the advanced araneids such as *Argiope argentata*. But, it captures mainly small prey by "Seize-Pull out" strategy, and does not use the swathes of silk for attack wrapping. So, the predatory behavior of this species should be situated in the new stage between the primitive stages and the advanced stages in the evolution of araneids' predatory behavior.

The predatory behavior of araneid spiders was reported by many authors (Peters, 1931, 1933; Robinson, 1969; Robinson, Mirick and Turner, 1969; Robinson and Olazzari, 1971; Robinson and Mirick, 1971; Robinson and Robinson, 1974; Robinson, 1975; Lubin, 1980). Robinson, Mirick and Turner (1969) assumed five stages in the evolutionary process of the predatory behavior of araneid spiders. They stated that in the earlier three stages the spiders use only biting to immobilize the prey and that in the later two stages they use both biting and wrapping for their prey immobilization. It was verified that the spiders included in the later stages (for example, *Argiope argentata*) use three predatory strategies (that is, Seize-Pull out, Bite-Wrap, Wrap-Bite).

Tetragnathid spiders are usually treated as a different family (Tetragnathidae) from Araneidae (BRISTOWE, 1958; YAGINUMA, 1960; LOCKET, MILLIDGE and MERETT, 1974; GERTSCH, 1979; KASTON, 1981), but are sometimes treated as a subfamily (Tetragnathinae) of Araneidae (COMSTOCK, 1940; LEVI, 1978). So, in any rate, they are closely related with araneids. But, as far as I know, the predatory behavior of tetragnathids has not been studied yet. So, I studied that of *Tetragnatha praedonia,* and compared it with that of araneids.

Consequently, it was verified that this species uses all the strategies which are used by the advanced araneids such as *Argiope argentata.* But, it was different from them for the following three points; that is, 1) the small size of the prey, 2) the low adhesiveness of the web, and 3) no use of the swathes of silk for the immobilization wrapping. The primitive araneids such as *Nephila clavipes* does not use the swathes of silk either. So, the predatory behavior of *T. praedonia* should be included into the new stage between the primitive stages and the advanced stages proposed by ROBINSON, MIRICK and TURNER (1969). I report these results here.

Materials and Methods

The investigation was done from June to October 1985 at several creeks flowing among the paddy fields in Nishigamo, Kita-ku, Kyoto City. *T. praedonia* had made their webs above the creeks (ca. 1 m in width). The investigation was done from evening till night when this species was hunting actively.

The prey captured by the webs were collected, identified and the body length was measured in laboratory. In the field, the behavior of the spiders and the prey were observed. The body length of the prey captured by the spiders were estimated by the eye.

Furthermore, in order to study the predatory behavior to large prey, butterflies (6-10 mm in body length), moths (15-25 mm), craneflies (5-40 mm) and damselflies (35-45 mm) were given to the webs, then the predatory behavior of the spiders to them was observed.

Results

1) Unit behavior consisting of predatory sequences

The unit behavior consisting of the predatory sequences, observed in the field and at the field experiment, were as follows;

Plucking; Thread-pulling behavior with legs I (Fig. 1A). When a prey hit the web, the spider oriented toward the prey, then pulled the radial threads with legs I. By the behavior, spider located the prey and perhaps estimated the size and the type of the prey. In many cases, spiders found the prey after plucking.

Running to prey; The approach from the hub to the capture site by running along the radial thread(s). It was frequently observed when the prey were struggling just after they struck the web.

Walking to prey; The approach to the capture site by walking along the radial thread(s). It was observed not only after plucking but also during searching for the un-located prey in the web.

Touch; The touch to the prey by legs I (and palps?). It was observed only once when capturing a butterfly.

Seizing in jaws; Seizing and holding the prey in the jaws (Fig. 1B). It was applied mainly to small prey, as states later. Just after this behavior, the spiders pulled the prey out of the web, then carried it in the jaws to the hub.

Biting; Biting the prey with jaws (Fig. 1C). It was observed at the capture site and the feeding site, at various stages of the predatory sequences (Table 1). When biting was applied as the first weapon (that is, as prey-immobilization), spiders ran to the prey and bit them rapidly. After the immobilization of prey, biting was also done at the capture site and the feeding site.

Table 1. Various types of biting and wrapping observed in the predatory behavior of *Tetragnatha praedonia*. X shows the behavior occured there.

	At Capture Site		At Hub or Web Margin (or out of Web)
	Immobilization (Attack)	Post-Immobilization	Post-Immobilization
Biting	X	X	X
Wrapping with Bite	—	X	X
Wrapping	X	X	X
Free Wrapping	—	X	X

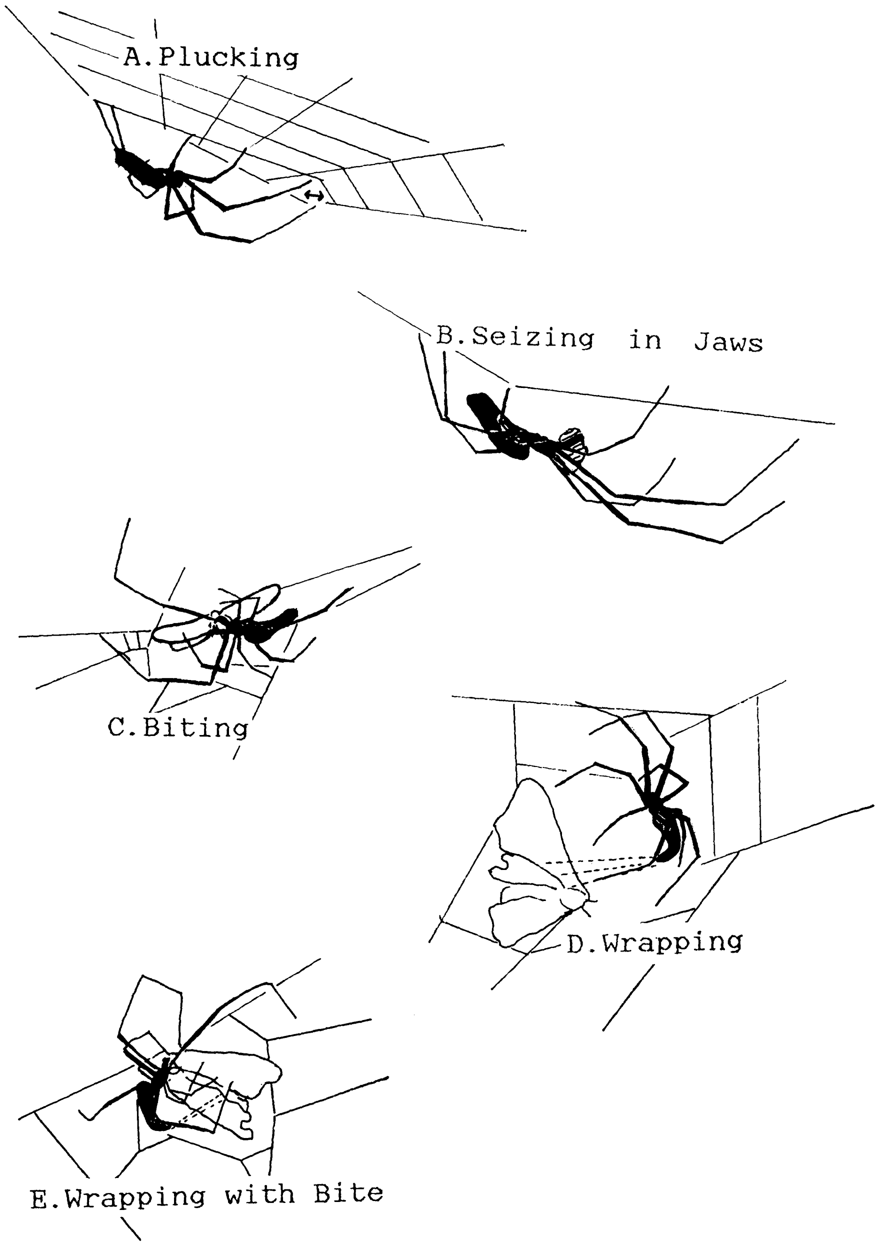

Fig. 1. Unit behavior of *T. praedonia*. See the text for the explanation.

Wrapping; Wrapping the prey with silk at a distance (Fig. 1D). The spider bent its abdomen, threw its silk aheads to the prey. It was frequently used for the post immobilization, but was sometimes used for prey-immobilization.

Wrapping with bite; Wrapping the prey with silk (the prey is being held or bitten with the jaws, Fig. 1E). The spider bent its abdomen, pulled its silk from its spinnerets, sent it ahead using legs IV alternatively, and threw it toward the prey. It was frequently observed at the capture site, but also sometimes observed at the feeding site. It occurred after immobilization biting (=attack biting) in most cases, but also sometimes occurred after post-immobilization wrapping or during feeding.

Free wrapping; Wrapping the prey with silk, rotating it with legs I and II after pulling-out or cutting-out. It was observed at the capture site and the feeding site.

Pulling out; Pulling the prey from the web, after seizing it in jaws. As states later, it was frequently applied to smally prey.

Cutting out; The removal of the prey by cutting the web. It was mainly applied to large prey. The threads entangling the prey were likely cut by the jaws and legs I. Spiders carried the prey to the feeding sites in most cases, but sometimes left them at the capture sites.

Carrying in jaws; Carrying the prey to feeding sites, holding it in the jaws after the removal of prey from the web. If the prey was small, the spider fell down with the dragline being attached to the hub, then climbed it up rapidly. It was only 2-4 seconds for the spider to capture a small prey and return with it. In the case of large prey, the spider returned to the feeding sites by walking beneath the web surface, seizing the prey in the jaws.

Carrying on silk; Carrying the prey to the feeding sites, being suspended on a silk line. It was applied to large prey.

Return to hub; The return of the spider to the hub by itself. At that time, the prey was left at the capture site.

Pulling prey from hub; Pulling the prey with legs I (and II?) from the hub. When prey was captured near the hub, the spider immobilized it by biting, and wrapped it. Then the spider returned to the hub alone, turned to the prey, and pulled it with legs I (and II?). The threads entangled the prey were cut by the spider, and the prey was suspended at the hub. This behavior was observed only once.

Suspension of prey at hub; The prey was sometimes suspended on a silk line at the hub. If the prey was large, it was suspended alone. But, if small prey were captured successively, the spider held several prey in the jaws, and packed them in a package with wrapping, then suspended it.

Feeding; Feeding was occurred at three sites; that is, the capture sites, the hub, and the web margins (or the scaffholds out of the web).

Note: Immobilization and post-immobilization are the categories proposed by ROBINSON, MIRICK and TURNER (1969). When wrapping is used as a initial means of restraint, they called it as "immobilization wrapping", on the other hand, they called all types of the wrapping as post-immobilization wrapping which occurred after the first attack (that is, immobilization). These categories were used by them also to biting.

2) Prey capture in fields

a) Kind and size of prey

As shows in Table 2, almost all prey collected from the webs were Diptera (especially midge fly). Most of them were small, and almost all prey were less than 3 mm in body length. Table 3 shows the body length distribution of the prey captured by spiders, and almost all prey were very small also in this case.

b) Capture efficiency of the prey struck to the webs

As shows in Table 4 and Fig. 2, 270 prey hit the webs (all prey were insects). In addition to these prey, there were many insects that passed through

Table 2. The kind and the body length of the prey collected in the webs of *Tetragnatha praedonia*.

	Body Length in mm						
	0-1	1-2	2-3	3-4	4-5	5-	Total
Midgeflies	32	123	45	5	0	0	205
Other nematocerous flies	1	5	2	0	1	2	11
Other Diptera	0	2	2	0	0	0	4
Aphids	0	1	0	0	0	0	1
Mayflies	0	0	0	0	3	2	5
Ants	0	0	1	0	0	0	1
Others	0	2	0	0	0	0	2
Total	33	133	50	5	4	4	229

Table 3. The body length of the prey fed by *Tetragantha praedonia*.

	Body length in mm					
	0-1.5	1.5-2.5	2.5-3.5	3.5-4.5	4.5-	Total
Number of prey	47	22	27	5	3	104

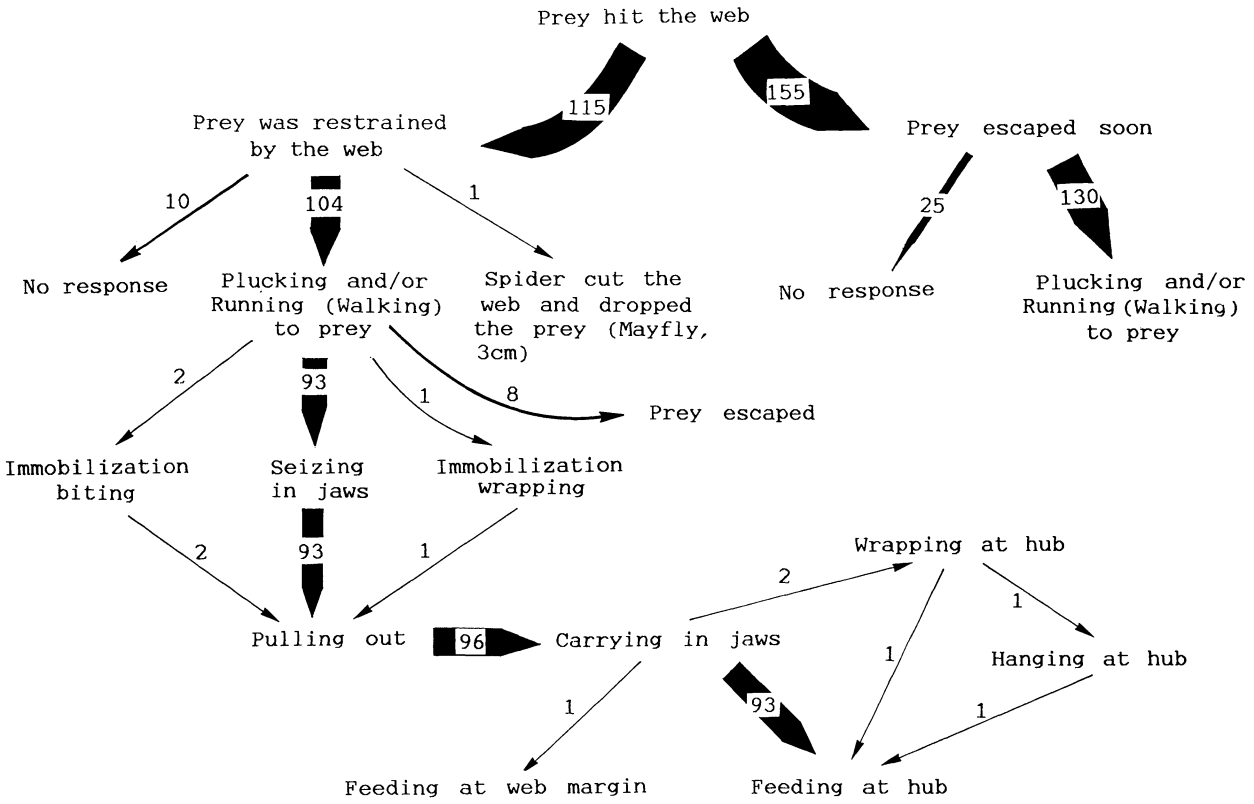

Fig. 2. The process of prey capture by *T. praedonia* observed above a brook.

Table 4. The efficiency of the prey capture by *Tetragnatha praedonia*.

Number of prey struck the web	270
Number of prey escaped	164 (60.7%)
Escaped for itself	155
Escaped by the movements of spiders	9
Number of prey captured by the webs	106 (39.3%)
Number of prey fed by spiders	96 (35.6%)

the web (among the threads), but I could not count the frequency. Of 270 prey, 164 individuals (60.7%) escaped from the webs. Its 94.5% (155 individuals) escaped for itself before spiders did not responce them, and the time of prey-restraint was short. Of 155 individuals which escaped by themselves, there were two types, that is, the prey which escaped just after the strike to the webs and those which escaped after the short time (less than several seconds) restraint by the viscid spirals, but these frequencies could not be counted. Remained 5.5% (9 individuals) were restrained rather rigidly by the webs, but could escape after the predatory behavior of spiders such as plucking. Probably, the prey could be released from the web by the vibration brought about by the predatory behavior. Of 9 prey, 8 prey were released by the plucking and/or running to prey, and a prey (mayfly, ca. 3 cm in body length) was fallen down by cutting-out of the web.

c) Predatory sequences and the frequencies

The predatory sequences, observed in the field, were as follows (Fig. 2). As stated earlier, the main prey were small insects. If the prey hit the web, the spider became alert, oriented toward it. Then, spiders selected either of the two behaviors, that is, plucking or the approach to the prey. After plucking, spiders always ran to the prey. Without plucking, spiders ran or walked to it. Then spiders attacked the prey with any of the three means, that is, seizing in the jaws, biting or wrapping. Seizing was used very frequently. It occurred almost momentarily, then the spider immediately pulled the prey from the web. In almost all cases of biting and wrapping, the prey were pulled out of the web by the jaws. All prey were carried in the jaws. Spiders fell down with the dragline being attached to the hub, then climbed it up rapidly, in almost all cases. In only one case, the prey was carried to the web margin, then fed there.

Wrapping at the hub before feeding was observed in capturing fairly large prey or in capturing several small prey successively. The former was a mayfly ca. 1 cm in length. In the latter case, the spider packed the newly-captured prey and several prey captured before into a package, then wrapped it there (Free wrapping).

3) Predatory sequences observed in field experiments

I gave large prey such as butterflies, moths, craneflies, and damselflies, to the webs of *T. praedonia*. Three types of the sequences were observed as shows in Figs. 3-5 (only successful examples were shown).

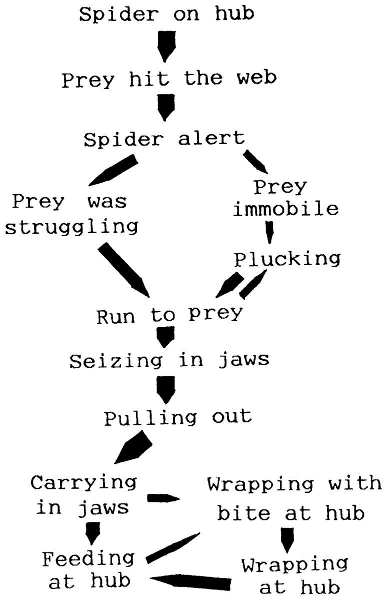

Fig. 3. "Seize-Pull out" strategy applied to three craneflies. The thickness of arrows shows the frequency of the behavior observed.

a) Seize-Pull out (Fig. 3); In this sequence, prey were seizing in the jaws, pulled from the webs, carried in the jaws, then fed at the hub. It was the same sequence observed in capturing smaller prey (1-3 mm in body length) in the field, as stated earlier. But, in this field experiments, the prey (craneflies) were always carried by walking (as shown earlier, smaller prey were carried by falling-down & climbing-up).

b) Bite-Wrap (Fig. 4); In this sequence, various patterns were observed. "Wrapping with bite" was observed in all cases, but "Wrapping", "Cutting out" and "Carrying" were not always observed in all cases. Furthermore, spiders sometimes returned to the hub alone, on the way to the predatory sequence. When the spider did not carry the prey, it was fed at the capture site.

There were three means of transportation, that is, 1) walking; the prey was being held in the jaws, 2) walking; the prey was being suspended from the spinnerets, 3) pulling the prey from the hub. Before feeding, "Biting", and "Wrapping" or "Wrapping with bite" at the hub or the web margin, were also observed.

c) Wrap-Bite (Fig. 5); This sequence was observed only for three times. In this sequence, there was a characteristic unit behavior, that is, "Try to bite". As the prey was strugglling violently, the spider could not immobilize by biting in spite of "Try to bite" for many times. Instead of the immobilization biting, then the spider attacked by wrapping repeatedly. But, the wrapping seemed to be of little use to immobilize the struggling prey, and the spider tried to bite

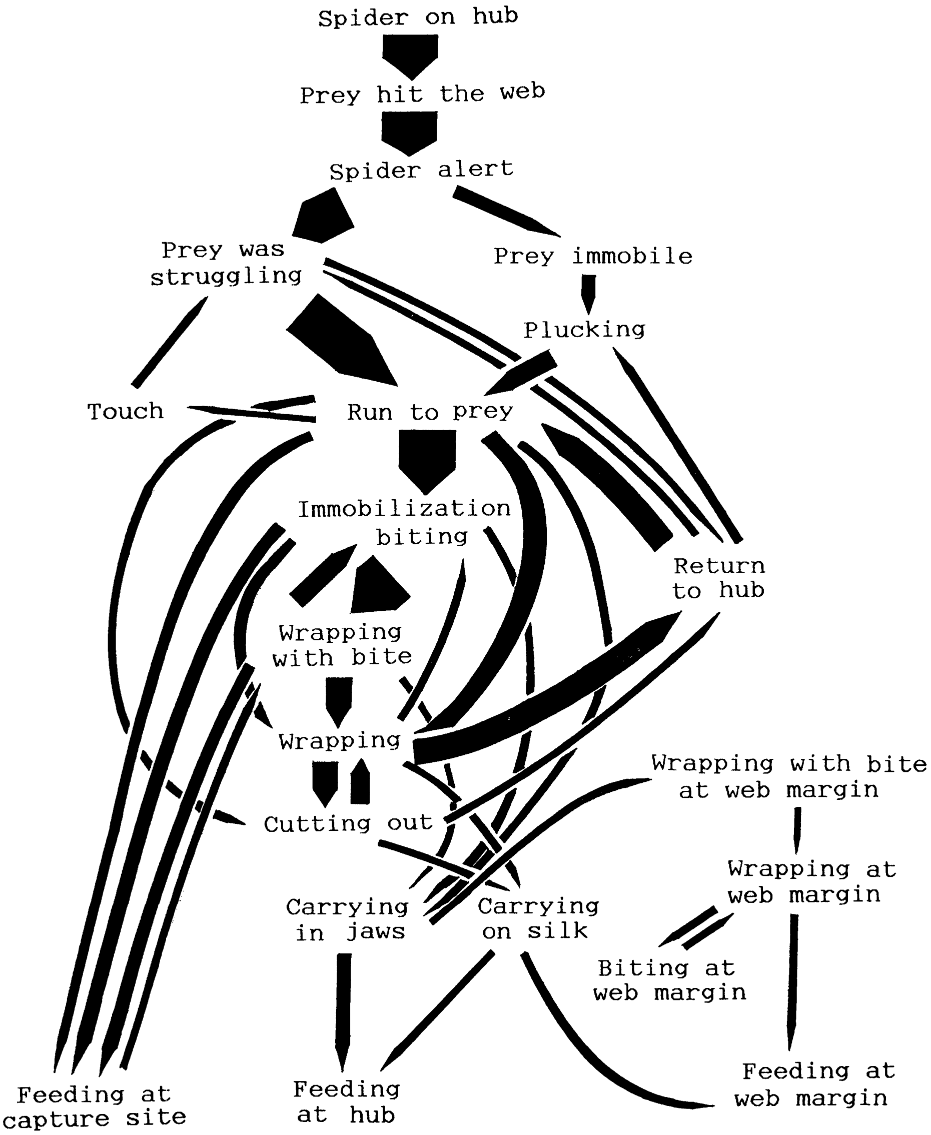

Fig. 4(A)

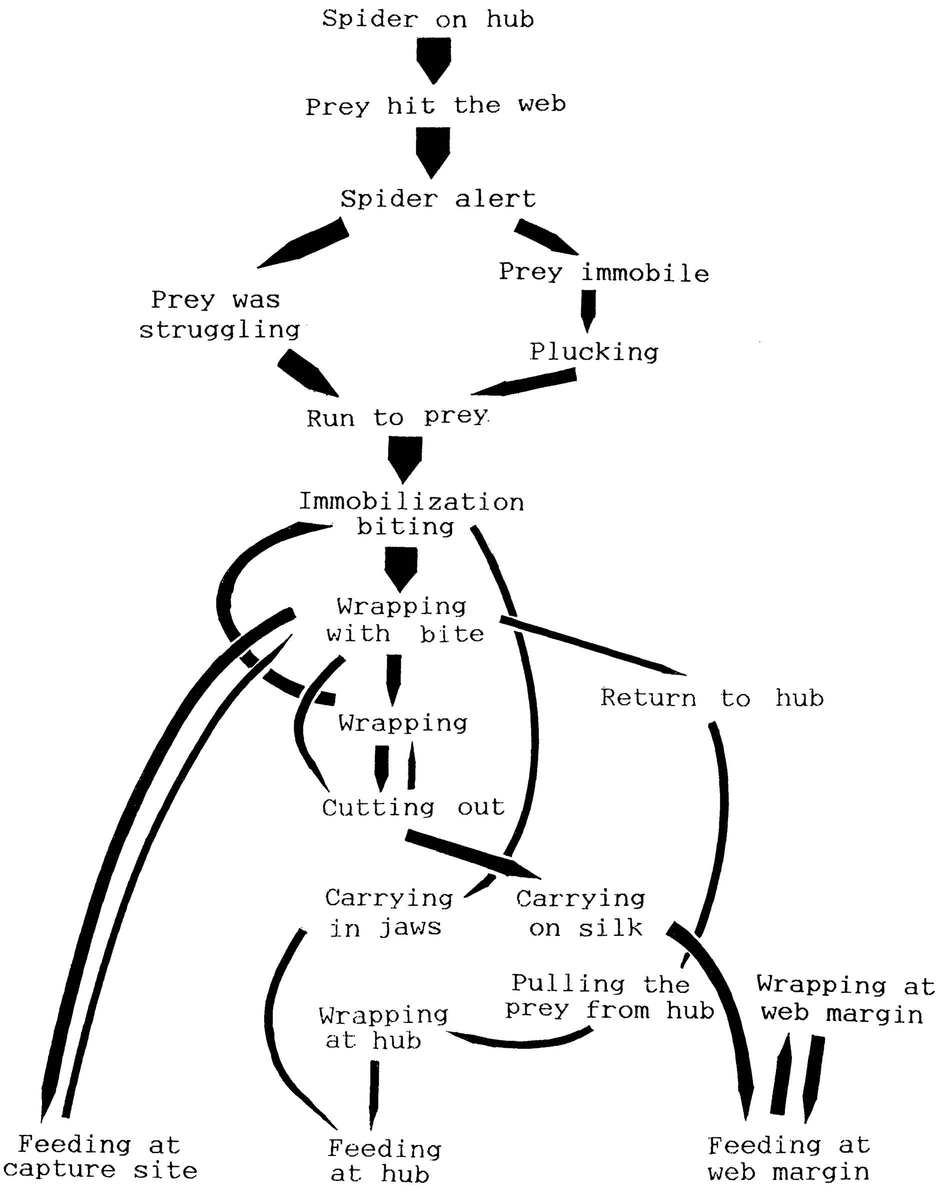

Fig. 4(B)

Fig. 4. "Bite-Wrap" strategy applied to nine Lepidoptera (4A) and to five individuals of craneflies and damselflies (4B).

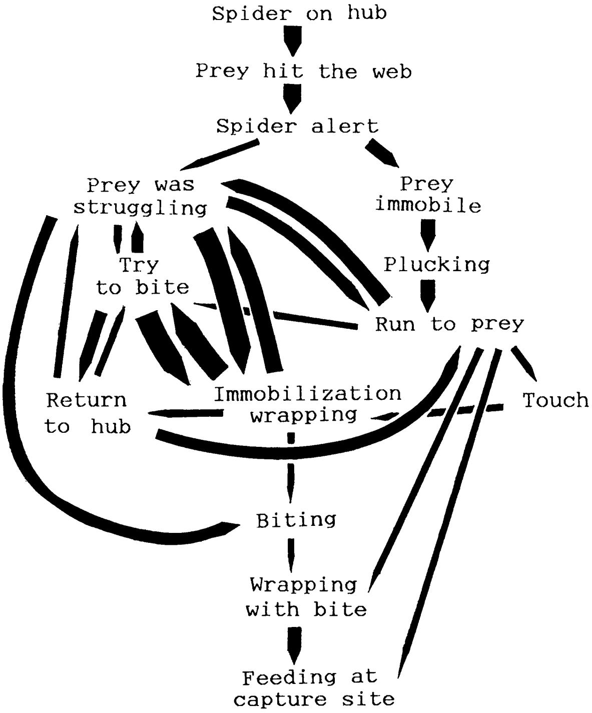

Fig. 5. "Wrap-Bite" strategy applied to a butterfly and two damselflies.

repeatedly among the wrapping. Sometimes, the spider returned alone the hub. Several prey escaped in this stage. In the successful three cases, the spider succeeded in the prey immobilization by biting after several trials of wrapping. These prey were always fed at the capture sites.

Table 5 summarizes the predatory sequences to the large prey given in the field experiments Butterflies escaped by flying or falling down from the web, before the spider approached to them. It was also observed that the spider did not bite because of the violent flutter of butterflies in spite of many trials to bite. In most cases, they escaped during the attack. After the escapes, a lot of scales of the butterflies were remained in the web. On the other hand, most of the craneflies and the damselflies were captured by spiders. Spiders did not apply "Seize-Pull out" to butterflies and moths, but in most cases they applied "Bite-Wrap" strategy. The latter strategy was sometimes applied also to the craneflies and the damselflies, but "Seize-Pull out" and "Wrap-Bite" were also

Table 5. The capture efficiency and the predatory strategies of *Tetragnatha praedonia* to large prey.

Kind of Prey (Body length in mm)	Number of Prey given (A)	Number of Prey captured (B)	B/A	Strategies		
				Seize-Pull out	Bite-Wrap	Wrap-Bite
Butterflies & Moths (6-25)	42	10	0.24	0	9	1
Craneflies & Dragonflies (5-45)	13	10	0.77	3	5	2
Total	55	20	0.36	3	14	3

Table 6. The relation between prey size (body length : BL) and predatory strategies.

Ratio of BL (Prey/Spider)	Predatory Strategy			
	Seize-Pull out	Bite-Wrap	Wrap-Bite	Total
0.0-0.2	56	0	0	56
0.2-0.4	38	0	0	38
0.4-0.6	3	7	1	11
0.6-0.8	0	2	0	2
0.8-1.0	0	0	0	0
1.0-1.5	1	3	0	4
1.5-2.0	0	1	0	1
2.0-	0	2	2	4
Total	98	15	3	116

Table 7. Relation between the predatory strategies and the feeding sites.

Strategies	Feeding Site			
	Hub	Web Margin & out of Web	Capture Site	Total
Seize-Pull out	98	0	0	98
Bite-Wrap	5	4	5	14
Wrap-Bite	0	0	3	3
Total	103	4	8	115

applied to them.

Table 6 shows the relation between the body length of prey and the predatory strategies, observed in the field and the field experiments. Apparently, "Seize-Pull out" was the strategy applied to small prey, on the other hand, "Bite-Wrap" and "Wrap-Bite" were the strategies applied to large prey. But, there was no clear difference in the body length of prey between the latter two strategies.

Table 7 shows the relation between the strategies and the feeding sites. Applying "Seize-Pull out", the spiders always carried the prey to the hub and fed there. On the contrary, applying to "Wrap-Bite", the spiders did not carry the prey and fed them at the capture sites. In the case of "Bite-Wrap", the spiders fed at various sites, that is, the hub, the web margins (or out of the web), and the capture sites. On the whole, almost all prey were fed at hub, because of the small size.

Discussion

Tetragnatha species make horizontal orb webs with an open hub, and adapt to capture small prey flying weakly (BRISTOWE, 1958; GERTSCH, 1979; KASTON, 1981; OKUMA and KUNIMI, personal communication). As stated in results, *T. praedonia* also captures mainly small Diptera (especially midge flies), and large prey are only sometimes captured by the web. Furthermore, many small prey which struck the web are restrained only momentarily. This fact suggests that it does not adapt to capture large prey. Many prey also escape from the web of *Leucauge magnifica*, belonging to another genus of Tetragnathidae, probably because of the less adhesiveness (YOSHIDA, unpublished data). So, the low capture efficiency may be common to tetragnathid orb-weaving spiders. Thus, because of the small size of prey and the low capture efficiency, they would be unable to get enough prey unless they make their webs where prey are very abundant. It may be due to such reason that many tetragnathids make their webs at damp habitats such as rivers, brooks, paddy fields, ponds, bogs and so on (BRISTOWE, 1958; GERTSCH, 1979; HAMAMURA, 1969; KAIHOTSU, 1973; KAYASHIMA, 1966; OKUMA, 1978; YAGINUMA, 1960; YAMANO and KIDO, 1975; YOSHIDA, 1981). At these habitats, weakly flying small prey such as midgefly and mayfly are very abundant (YOSHIDA, 1977).

EBERHARD (1967) stated that the advanced stage in the evolution of predatory behavior of spiders is characterized by "capturing and subduing prey from a distance by applying silk to it". ROBINSON and his colleagues intensively studied the predatory behavior of some araneids, such as *Argiope argentata* and *Nephila clavipes*, and verified that there are three types of predatory sequences, that is, "Seize-Pull out", "Bite-Wrap" and "Wrap-Bite" (ROBINSON, 1969; ROBINSON, MIRICK and TURNER, 1969; ROBINSON and OLAZARRI, 1971; ROBINSON and MIRICK, 1971; ROBINSON and ROBINSON, 1974; ROBINSON, 1975; ROBINSON and ROBINSON, 1976).

Furthermore, they assumed five stages in the evolutionary process of the predatory behavior of araneid spiders. By their opinion, only biting is used for prey immobilization in the earlier three stages. Several araneid spiders, such as *Nephila clavipes*, some species of *Micrathena* and *Gasteracantha*, are included in the stages. But, in the later two stages, not only biting but also wrapping are used for prey immobilization. *Argiope* spp., *Araneus diadematus*, and *Eriophora* sp. are included in the stages (ROBINSON, MIRICK and TURNER, 1969). In almost all cases, *T. praedonia* immobilizes its prey by biting (including seizing in jaws) in natural conditions. So, this species may be included in the earlier stages. But, as this species sometimes uses "Wrap-Bite" strategy to large prey given artificially, though the "immobilization wrapping" has less effect to restrain the prey, it should not be included in the earlier stages.

On the other hand, the species included in later stages use their swathes of silk for prey-immobilization, unless the prey is Lepidoptera (which is immobilized by biting). Thus, the development of the swathes of silk does characterize the later stages. But, *T. praedonia* seems not to use its swathes of silk. The silk pulled from the spinnerets of the species is fine and can not be clearly seen unless the observer throws strong light on it. So, it would be unsuitable that the predatory behavior of *T. praedonia* is included in the later stages.

There are also other differences between *T. praedonia* and the advanced araneids such as *Argiope*. For example, *Argiope* spp. immobilize the prey mainly by wrapping, on the other hand *T. praedonia* immobilize the prey mainly by seizing and biting. This difference is partly due to the difference in the size of the prey captured by their webs. The prey of *T. praedonia* are very small, but the prey of *Argiope* are fairly large (MURAKAMI, 1983; ROBINSON and ROBINSON, 1970). As both spiders apply "Seize-Pull out" strategy to small prey, so it is a matter of course that *T. praedonia* frequently uses this strategy and that *Argiope* does not use it so much. But, this is not due to the difference only in the prey size. As shown in results, the attack wrapping of *T. praedonia* is the responce after the spider did not succeed in its attack biting, on the other hand, *Argiope* uses its attack wrapping soon after the discrimination of the prey type (ROBINSON, 1969). So, the attack wrapping of *T. praedonia* should be discriminated from that of *Argiope*. Judging from the observation of the predatory behavior, *T. praedonia* is unlikely to discriminate the prey type, such as craneflies, damselflies and butterflies, from each other. This species intends to bite all the prey in spite of the prey type.

Furthermore, "Wrapping with bite" observed after immobilization bite at the capture site also characterize the predatory behavior of this species (or genus *Tetragnatha*?) because of the high frequency (*Argiope argentata* rarely shows such unit behavior, ROBINSON and OLAZARRI, 1971). *T. praedonia* does not carry its prey to the hub in some cases, but feeds at the capture sites or at the web margins (or out of the web). As araneids do not show such kinds of behavior, they would be also the specific behavior to *T. praedonia*. But, the function of the feeding at the sites except the hub is not known. A hub is the center of orb web, and is likely to be the best site to perceive the fluctuation brought about by the prey. So, in order to capture the next prey which strikes the web soon after the first prey, it is desirable for the spider to reduce the time absent from the hub as far as possible. In natural conditions, *T. praedonia* seems to show such strategy; that is, it takes only 2-4 seconds for the spider to be absent from the hub to capture small prey. On the contrary, in the case of capturing large prey, the spider seems not to take this strategy; that is, it takes long time for capturing the prey, and the spider used to ignore small prey restrained by the web after the large prey. So, the feeding on large prey at the sites except the hub may mean that the spider needs not more prey because of the full stomach.

In conclusion, the predatory behavior of *T. praedonia* should be situated in the new stage between the earlier three stages and the later two stages, proposed by ROBINSON, MIRICK and TURNER (1969). This stage is characterized by the lack of the swathes of silk and by the early form of the attack wrapping. If *T. praedonia* becomes to use the swathes of silk for prey-immobilization, the predatory behavior will become simmilar to that of advanced araneids, such as *Argiope argentata*.

Of course, it does not mean that *T. praedonia* should be situated in the process of the evolution from primitive araneids (such as *Nephila clavipes*) to advanced araneids. Tetragnathids and araneids have evolved along the different routes, though both are relatively related with each other. I can only say that there may be such a intermediate stage also in the evolution of the predatory behavior of araneids.

Recently, I knew another intermediate stage; that is, a Japanese *Nephila*, *N. clavata*, uses the swathes of silk but does not use for prey-immobilization (SHINKAI, unpublished data). He stated that the swathes are very thin and can be hardly seen. If the species becomes to use the swathes of silk for prey-immobilization, its predatory behavior will resemble that of advanced araneids. So, in conclusion, there are two intermediate stages.

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摘　　要

吉田　真（立命館大学理工学部生物地学教室，〒603 京都市北区等持院北町 56-1）：アシナガグモの捕食行動。

自然状態および餌を与えた場合のアシナガグモの捕食行動を観察した。自然状態では，この種はおもにユスリカなど体長3ミリ以下の双翅類昆虫を捕食していた。クモは通常，網の引き（Plucking）によって餌の所在を確認し，走り寄って上顎で餌をくわえ（Seizing），網から引き離して（Pulling out），餌をコシキに運び，摂食した（Seize-Pull out 戦略）。与えられた大きな餌に対して，クモは Seize-Pull out 戦略を含む3つの戦略を使用した。鱗翅類は多くの場合 Bite-Wrap 戦略によって，ガガンボとトンボは Seize-Pull out, Bite-Wrap, Wrap-Bite の3つの戦略によって，それぞれ捕獲された。Bite-Wrap 戦略においては，餌はまず Bite によって固定（immobilization）され，その後で糸を巻き付けられた（Wrapping）。これに対して Wrap-Bite 戦略においては，餌はまず Wrapping によって攻撃され，その後で Biting が行われた。

餌のタイプを識別したこのような捕食戦略の違いのもつ意味や，捕食行動の進化の過程において，この種が占める位置について考察した。

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